

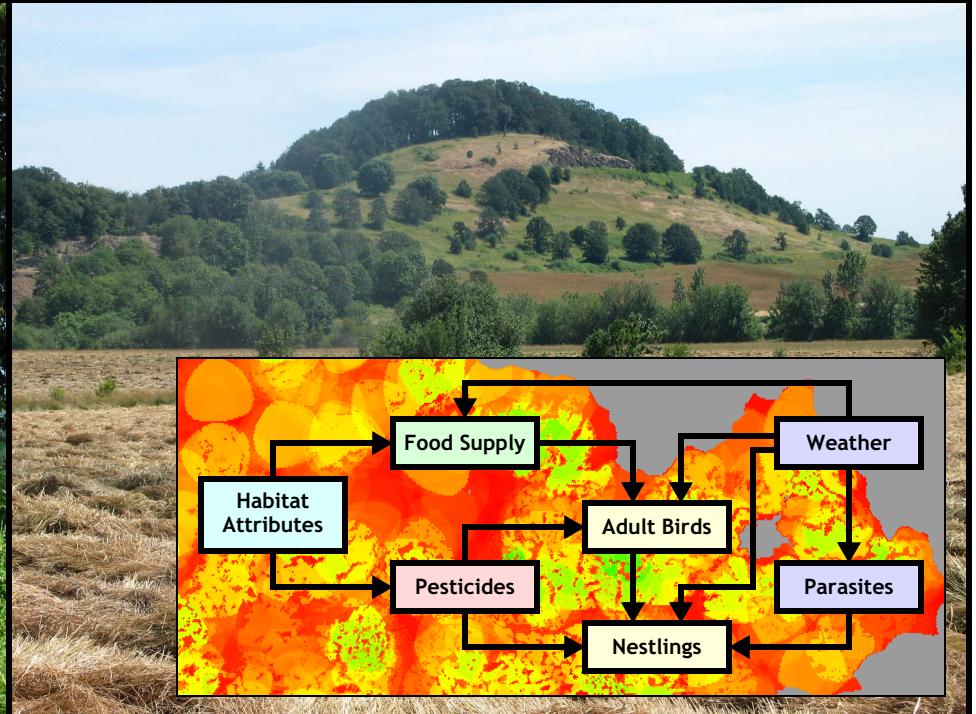
Landscape Connectivity Source-Sink Dynamics, and Population Viability



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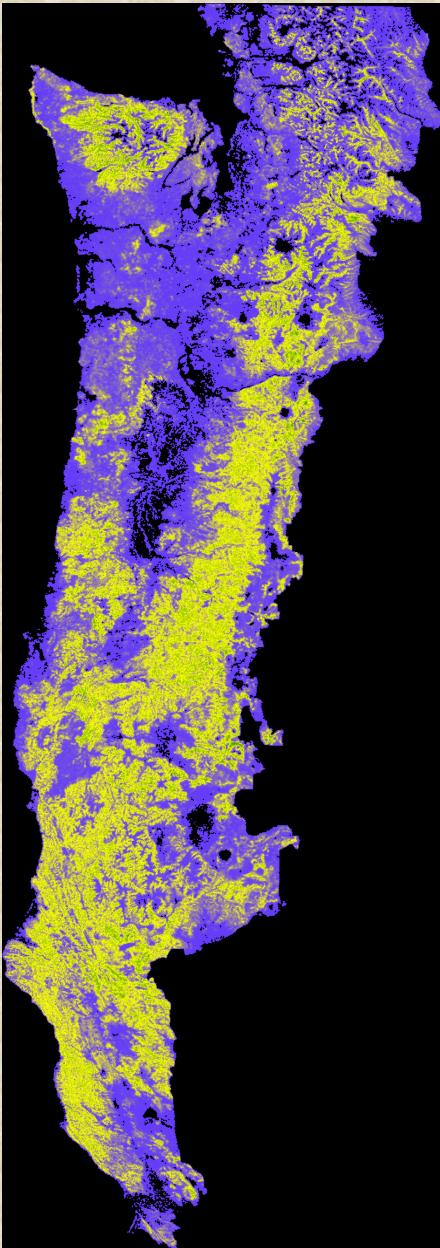


The Subject of this Talk

- The importance of connectivity & source-sink dynamics are widely appreciated.
- Tools for measuring these features have limited biological and ecological realism.
- The methodology described here makes it possible to measure landscape connectivity and source-sink dynamics without having to simplify the model system.

Sources and Sinks

- Sources are net *producers* of members of a population.
- Sinks are net *consumers* of members of a population.
- Whether an area is a source or a sink depends on the balance of birth, death emigration, and immigration rates
- The impact a source or sink will have also depends on its neighborhood, and on its connectivity to surrounding sites

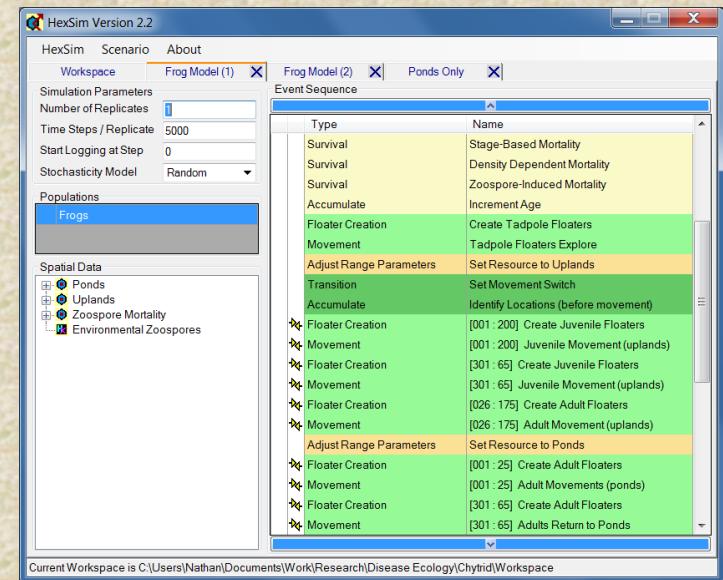
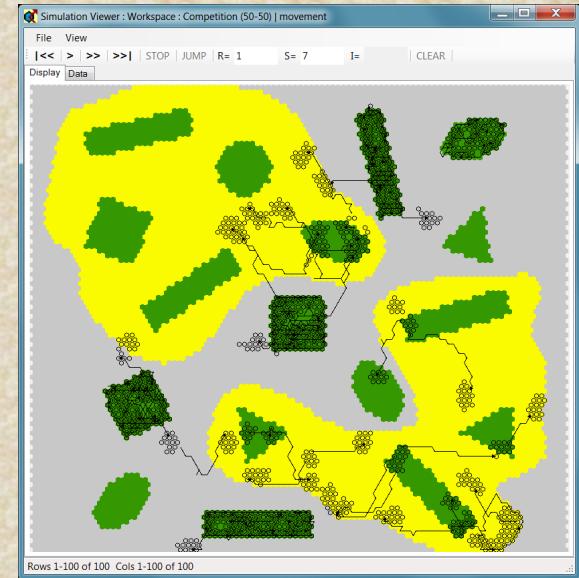


Identifying & Quantifying Sources and Sinks can be Difficult in Practice

- Where does one patch end and another begin?
- Which parts are connected and which are isolated?
- How do we know which are sinks and which are sources?
- How important is one location relative to another?

I'll Describe an Approach that Doesn't Rely On Simplifying Assumptions...

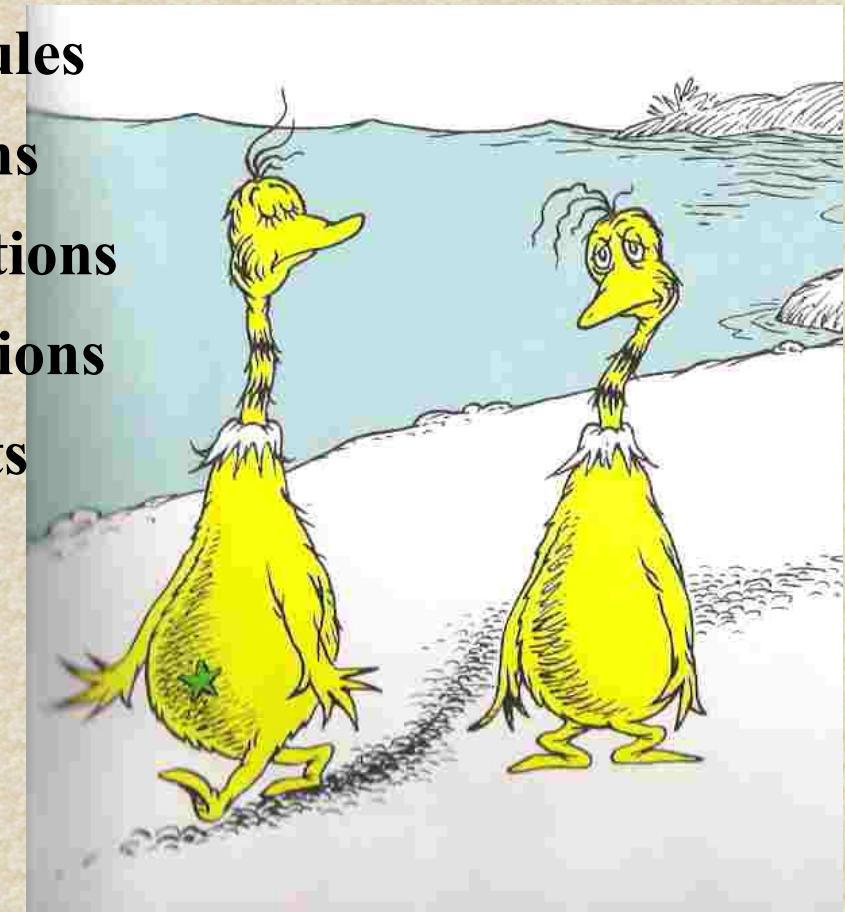
- HexSim is a new computer simulation model.
- It was designed for quantifying wildlife population response to multiple interacting stressors.
- HexSim can evaluate sources, sinks and connectivity without simplifying landscapes, species' life histories, or disturbance regimes.



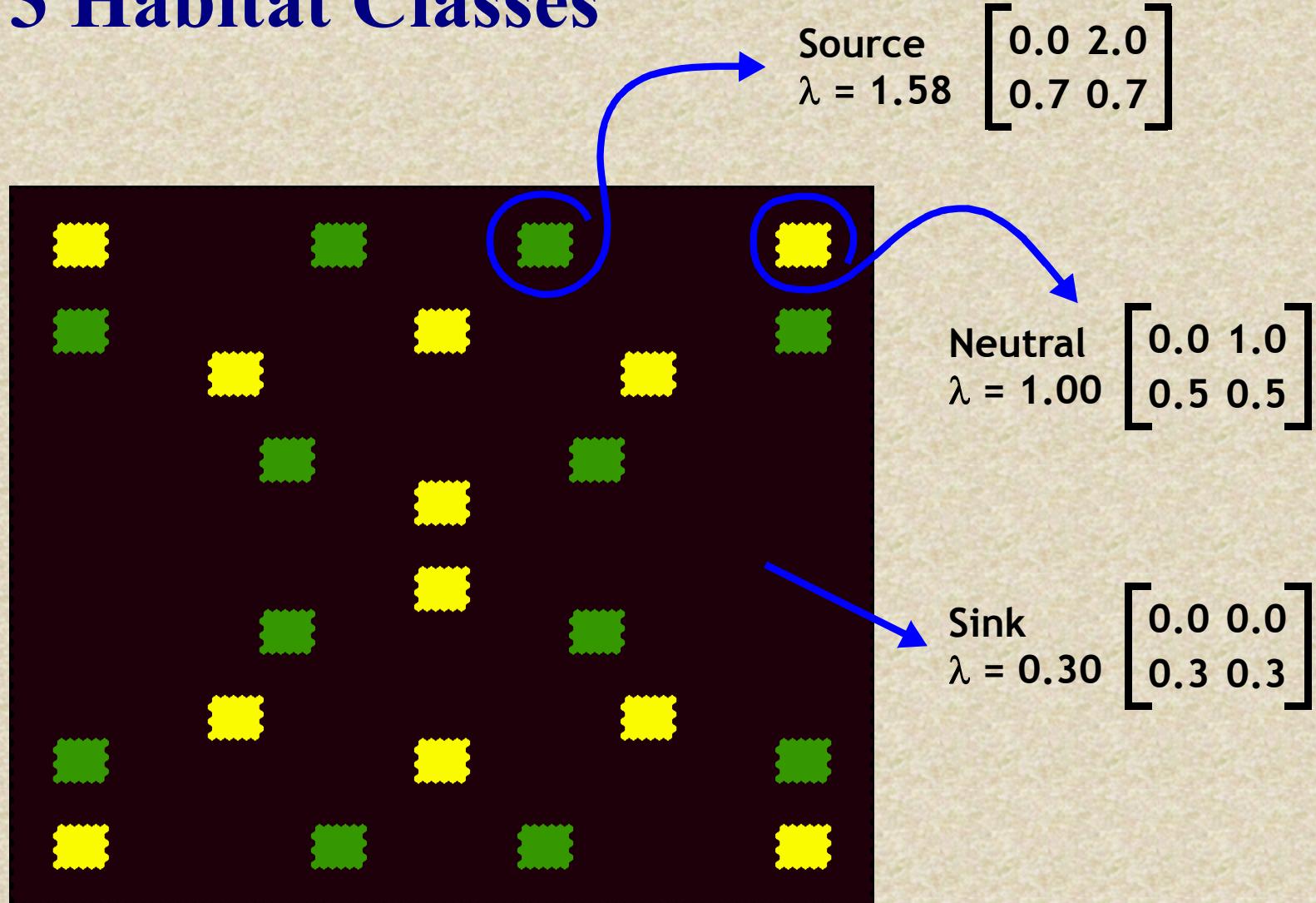
HexSim Fundamentals

- Spatially-Explicit and Individual-Based
- Landscapes can Change Continuously
- No Built-In Assumptions or Rules
- Multi-Stressor with Interactions
- Multi-Population with Interactions
- Females-only or 2-Sex Simulations
- Life History Stratified by Traits
- Includes Landscape Genetics

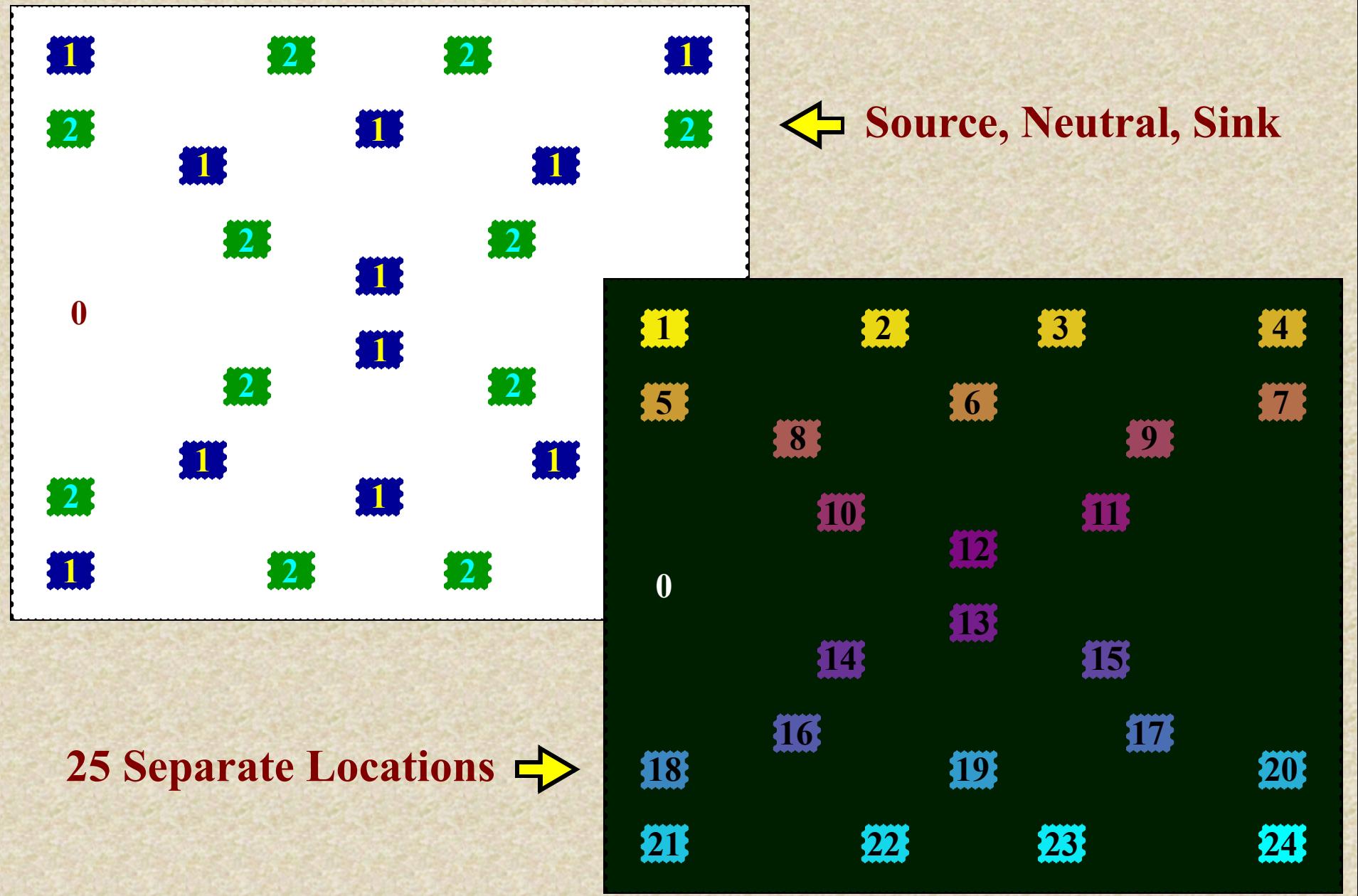
www.hexsim.net

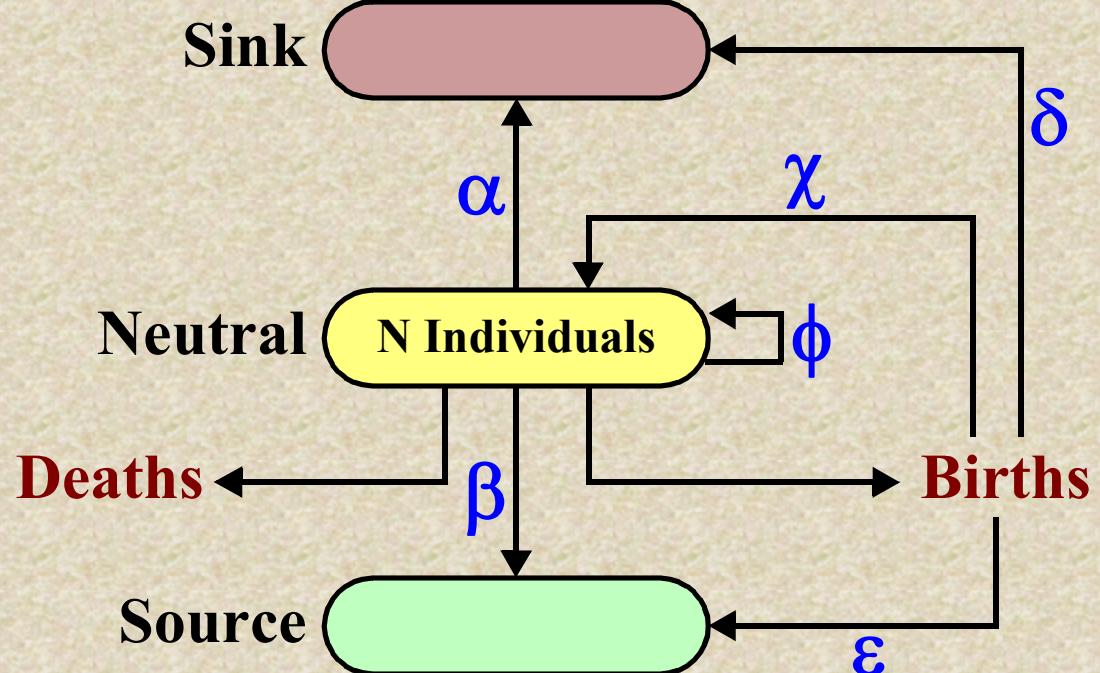


Start with a Simple Example: 3 Habitat Classes



Identify One or More Spatial Sampling Schemes

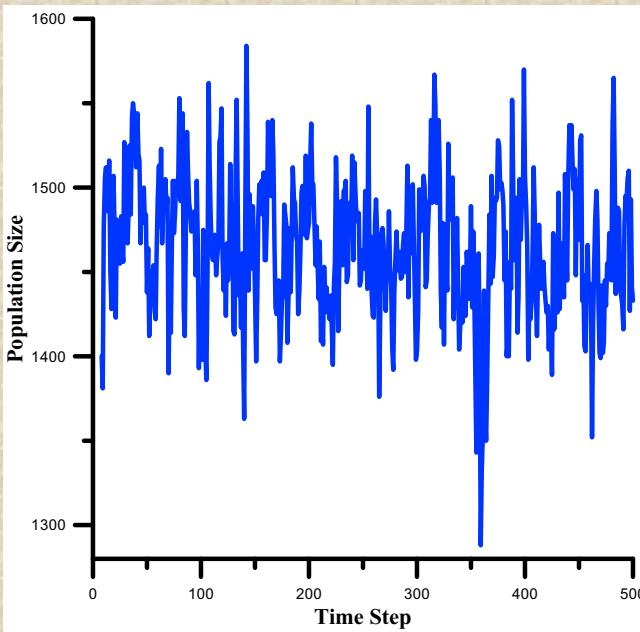
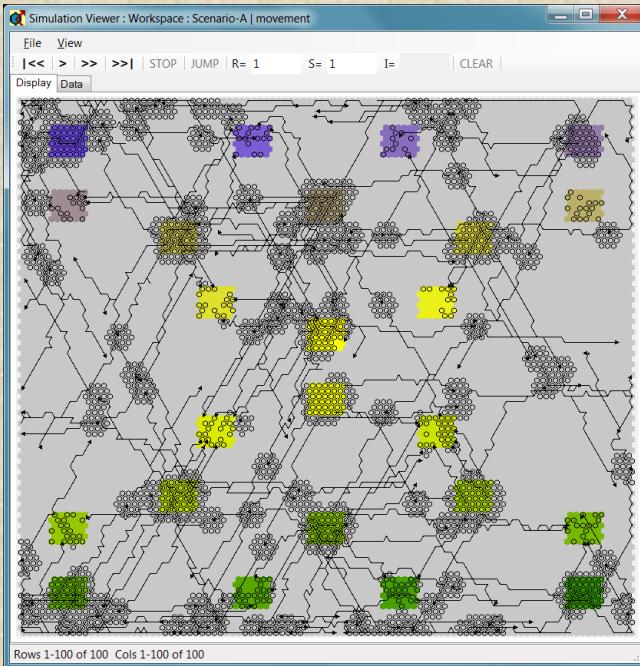




| | | From | | |
|----|---------|------|--|--------|
| | | Sink | Neutral | Source |
| To | Sink | | $\Sigma (\alpha + \delta) / \Sigma N$ | |
| | Neutral | | $\Sigma (\phi + \chi) / \Sigma N$ | |
| | Source | | $\Sigma (\beta + \epsilon) / \Sigma N$ | |

Computing Matrix Values

- ❑ A year begins with N individuals in the location of interest (here, Neutral).
- ❑ The N individuals move, reproduce, and die. But only those who acquire sufficient resources are allowed to reproduce.
- ❑ HexSim tallies up all of the different transitions. This is repeated for every location, year, replicate.
- ❑ The tallies are divided by the sum (over year and replicate) of the N values.
- ❑ Column sums equal total location productivity. A productivity of 1.0 divides sources from sinks.



Results for the 3 Classes

- Fluxes are used to construct a projection matrix. The matrix can be used to compute lambda.
- Connectivity and source-sink properties can be read directly off the matrix.

Flux Probabilities

| Lambda = 1.0000 | | From | | |
|-----------------|---------|--------|---------|--------|
| | | Sink | Neutral | Source |
| To | Sink | 0.1814 | 0.3584 | 0.6486 |
| | Neutral | 0.0741 | 0.4310 | 0.3051 |
| | Source | 0.0449 | 0.0857 | 0.8930 |
| Column Sums | | 0.3005 | 0.8751 | 1.8466 |

Results for all 25 Sites

- Lambda is unchanged. But the matrix now has the background sink, 12 neutral, and 12 source areas.
- All the neutral areas, and some of the anticipated sources, end up functioning as demographic sinks.
- The matrix reflects a highly-connected landscape.

| Lambda = 1.0000 | | | | | | | | | | | | | | | | | | | | | | | | | |
|-----------------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|
| | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 |
| 0 | 0.1814 | 0.3555 | 0.6799 | 0.6820 | 0.3499 | 0.7157 | 0.2880 | 0.7245 | 0.4035 | 0.3969 | 0.5513 | 0.5480 | 0.3518 | 0.3497 | 0.5579 | 0.5491 | 0.3990 | 0.4022 | 0.7188 | 0.2994 | 0.7018 | 0.3570 | 0.7036 | 0.6748 | 0.3492 |
| 1 | 0.0071 | 0.3606 | 0.1140 | -- | -- | 0.1399 | 0.0010 | -- | 0.0213 | -- | 0.0075 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 2 | 0.0030 | 0.0526 | 0.8286 | 0.0328 | -- | 0.0204 | 0.0052 | -- | 0.0093 | 0.0004 | 0.0097 | 0.0039 | 0.0284 | 0.0003 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 3 | 0.0028 | -- | 0.0348 | 0.8305 | 0.0517 | -- | 0.0058 | 0.0185 | 0.0007 | 0.0109 | 0.0042 | 0.0099 | 0.0257 | 0.0003 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 4 | 0.0072 | -- | -- | 0.1205 | 0.3453 | -- | 0.0010 | 0.1382 | -- | 0.0185 | -- | 0.0080 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 5 | 0.0048 | 0.0527 | 0.0129 | -- | -- | 0.7992 | 0.0271 | -- | 0.0107 | -- | 0.0082 | -- | -- | 0.0536 | -- | 0.0001 | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 6 | 0.0058 | 0.0008 | 0.0644 | 0.0548 | 0.0016 | 0.0573 | 0.3015 | 0.0600 | 0.0248 | 0.0256 | 0.0289 | 0.0281 | 0.0089 | 0.0052 | 0.0730 | 0.0728 | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 7 | 0.0050 | -- | -- | 0.0135 | 0.0546 | -- | 0.0274 | 0.7978 | -- | 0.0111 | -- | 0.0082 | -- | -- | 0.0511 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 8 | 0.0057 | 0.0153 | 0.0953 | 0.0024 | -- | 0.0512 | 0.0216 | -- | 0.4590 | 0.0042 | 0.1306 | 0.0025 | 0.0048 | 0.0121 | 0.0140 | -- | 0.0005 | -- | 0.0001 | -- | -- | -- | -- | -- | -- |
| 9 | 0.0060 | -- | 0.0034 | 0.0988 | 0.0142 | -- | 0.0203 | 0.0498 | 0.0052 | 0.4530 | 0.0033 | 0.1262 | 0.0058 | 0.0101 | -- | 0.0119 | -- | 0.0001 | -- | -- | 0.0001 | -- | -- | -- | -- |
| 10 | 0.0032 | 0.0043 | 0.0102 | 0.0033 | -- | 0.0077 | 0.0033 | -- | 0.0123 | 0.0011 | 0.7580 | 0.0725 | 0.0063 | 0.0041 | 0.0040 | 0.0008 | 0.0039 | -- | 0.0533 | 0.0392 | -- | -- | -- | -- | -- |
| 11 | 0.0033 | -- | 0.0032 | 0.0104 | 0.0057 | -- | 0.0040 | 0.0062 | 0.0012 | 0.0148 | 0.0724 | 0.7602 | 0.0048 | 0.0036 | 0.0009 | 0.0026 | -- | 0.0047 | -- | 0.0325 | 0.0549 | -- | -- | -- | -- |
| 12 | 0.0054 | -- | 0.0553 | 0.0499 | -- | -- | 0.0077 | -- | 0.0036 | 0.0057 | 0.0555 | 0.0549 | 0.3696 | 0.0389 | 0.0236 | 0.0246 | 0.0049 | 0.0049 | -- | 0.0042 | -- | -- | 0.0008 | 0.0006 | -- |
| 13 | 0.0051 | -- | 0.0008 | 0.0008 | -- | -- | 0.0040 | -- | 0.0056 | 0.0050 | 0.0264 | 0.0268 | 0.0357 | 0.3621 | 0.0535 | 0.0548 | 0.0048 | 0.0055 | -- | 0.0084 | -- | -- | 0.0460 | 0.0548 | -- |
| 14 | 0.0032 | -- | 0.0001 | -- | -- | 0.0526 | 0.0366 | -- | 0.0045 | -- | 0.0036 | 0.0008 | 0.0036 | 0.0051 | 0.7606 | 0.0733 | 0.0124 | 0.0007 | 0.0075 | 0.0040 | -- | 0.0044 | 0.0096 | 0.0033 | -- |
| 15 | 0.0033 | -- | -- | -- | -- | 0.0385 | 0.0517 | -- | 0.0044 | 0.0011 | 0.0030 | 0.0053 | 0.0044 | 0.0756 | 0.7565 | 0.0013 | 0.0135 | -- | 0.0044 | 0.0058 | -- | 0.0035 | 0.0095 | 0.0047 | |
| 16 | 0.0061 | -- | -- | -- | -- | 0.0001 | -- | -- | 0.0004 | -- | 0.0146 | -- | 0.0096 | 0.0049 | 0.1256 | 0.0028 | 0.4454 | 0.0046 | 0.0507 | 0.0187 | -- | 0.0137 | 0.1006 | 0.0029 | -- |
| 17 | 0.0058 | -- | -- | -- | -- | -- | -- | -- | 0.0006 | -- | 0.0134 | 0.0110 | 0.0059 | 0.0023 | 0.1324 | 0.0049 | 0.4545 | -- | 0.0221 | 0.0483 | -- | 0.0024 | 0.0957 | 0.0130 | |
| 18 | 0.0053 | -- | -- | -- | -- | -- | -- | -- | 0.0001 | -- | 0.0517 | -- | -- | -- | 0.0074 | -- | 0.0098 | -- | 0.7957 | 0.0267 | -- | 0.0576 | 0.0133 | -- | |
| 19 | 0.0057 | -- | -- | -- | -- | -- | -- | -- | -- | 0.0748 | 0.0720 | 0.0044 | 0.0064 | 0.0276 | 0.0289 | 0.0247 | 0.0245 | 0.0596 | 0.2981 | 0.0614 | 0.0021 | 0.0572 | 0.0612 | 0.0007 | |
| 20 | 0.0050 | -- | -- | -- | -- | -- | -- | -- | 0.0001 | -- | 0.0514 | -- | -- | -- | 0.0092 | -- | 0.0090 | -- | 0.0273 | 0.7983 | -- | -- | 0.0162 | 0.0511 | -- |
| 21 | 0.0069 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 0.0083 | -- | 0.0176 | -- | 0.1385 | 0.0006 | -- | 0.3524 | 0.1223 | -- | -- | |
| 22 | 0.0030 | -- | -- | -- | -- | -- | -- | -- | -- | -- | 0.0007 | 0.0204 | 0.0103 | 0.0035 | 0.0114 | 0.0013 | 0.0184 | 0.0048 | -- | 0.0513 | 0.8338 | 0.0325 | -- | -- | |
| 23 | 0.0029 | -- | -- | -- | -- | -- | -- | -- | -- | -- | 0.0005 | 0.0281 | 0.0042 | 0.0098 | 0.0008 | 0.0096 | -- | 0.0055 | 0.0179 | -- | 0.0320 | 0.8303 | 0.0531 | -- | |
| 24 | 0.0073 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 0.0075 | -- | 0.0215 | -- | 0.0011 | 0.1486 | -- | -- | 0.1151 | 0.3526 | -- |

Methodology in Summary

The sampling schemes can have absolutely no impact on the simulation dynamics !!!

Two types of projection matrices contain:

- ➔ Raw count data
- ➔ Transition probabilities

Source-sink properties obtained from:

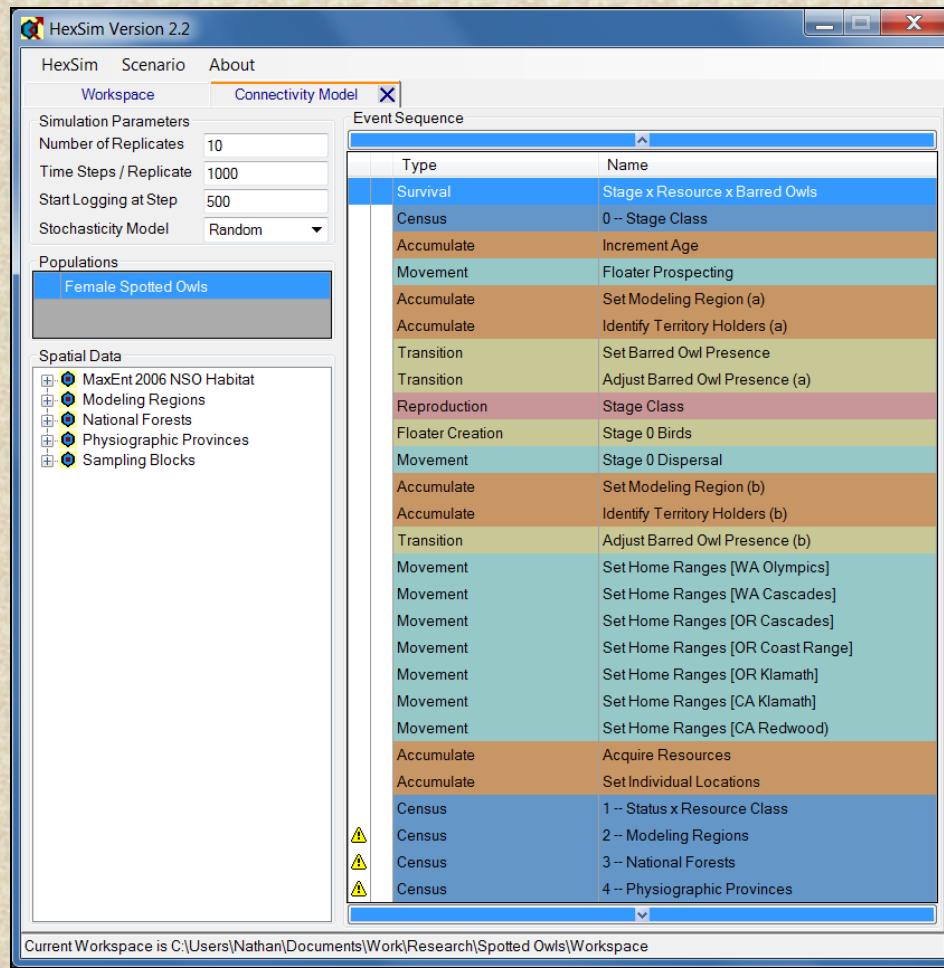
- ➔ Productivity report [births - deaths]
- ➔ Projection matrix [$E - I = \text{col sum} - \text{row sum}$]

Connectivity assessed from projection matrix

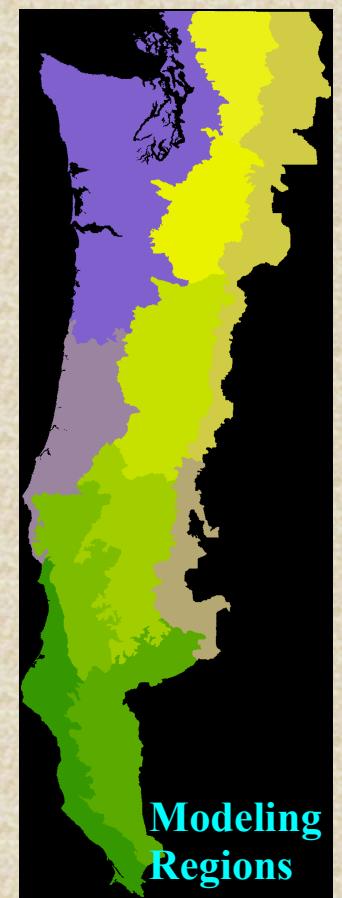
- ➔ From direct inspection of the matrix elements
- ➔ From a variety of numerical techniques

An Application: Northern Spotted Owls

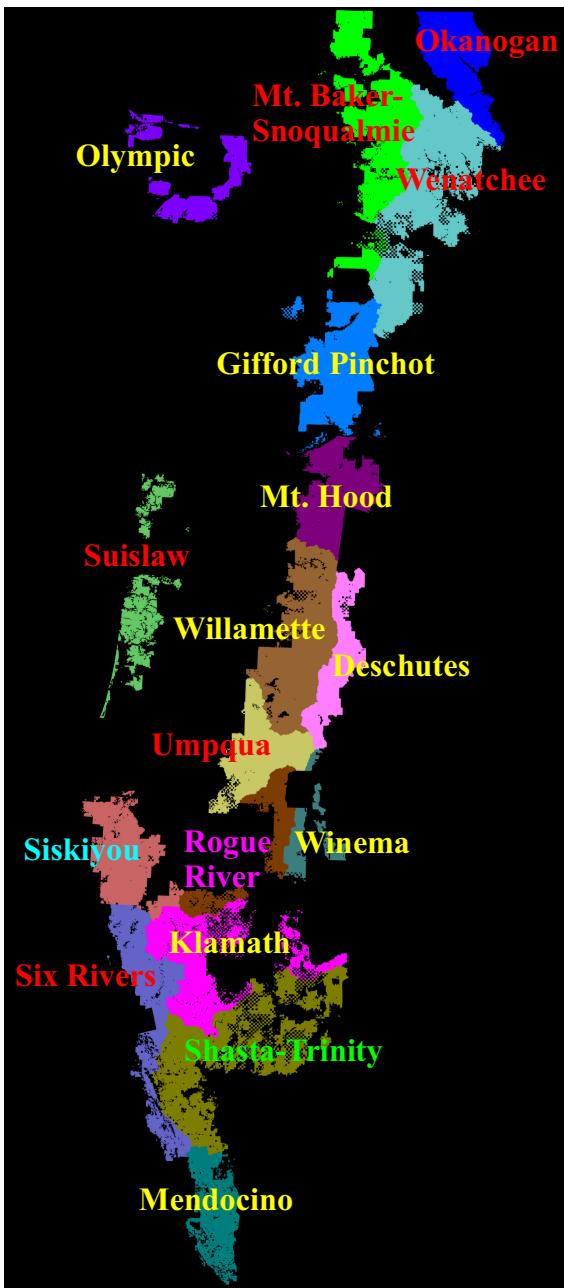
This HexSim simulation forms the basis of the latest US FWS spotted owl recovery plan.



The study area covers the U.S. range of the owl, from northern California to the top of Washington.



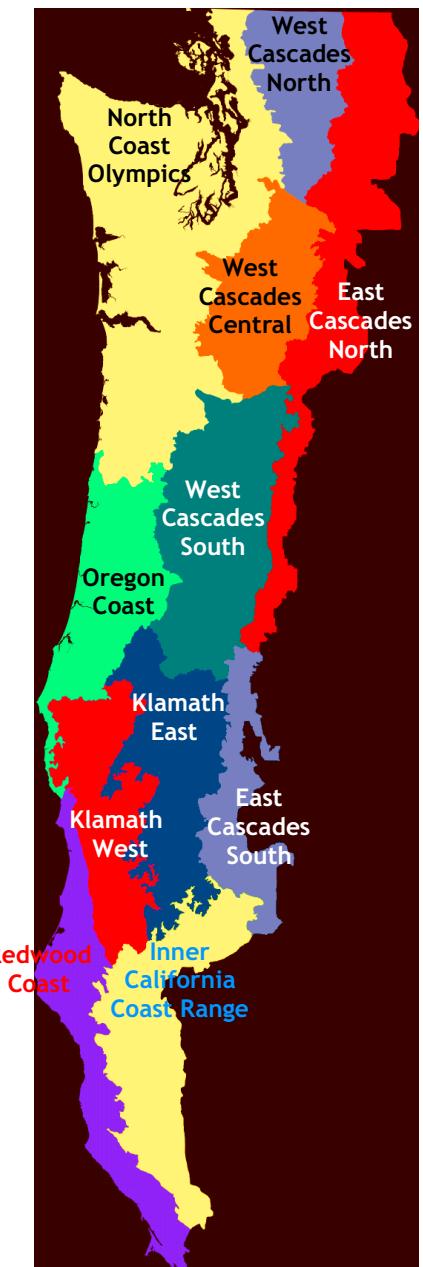
17 National Forests



Simulation Details

- Sampled locations include National Forests, modeling regions, and sampling blocks.
- The sampling blocks map has 5434 separate locations.
- Productivity (source-sink value) and connectivity matrices were generated for every location.
- Landscape performance can be evaluated at multiple scales simultaneously.
- Relationships between source-sink quality and connectivity can be explored.

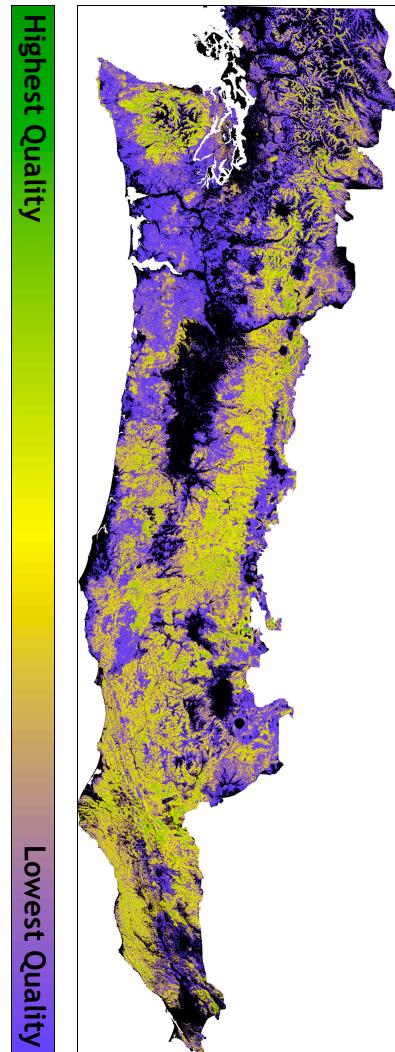
11 Modeling Regions



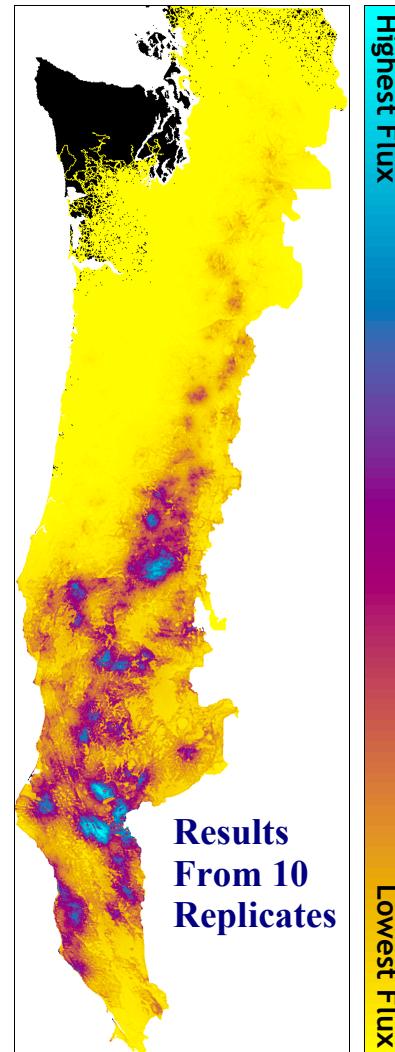
Hexagon Scale

5434 Sampling Blocks
(10 x 10 Hexagon)

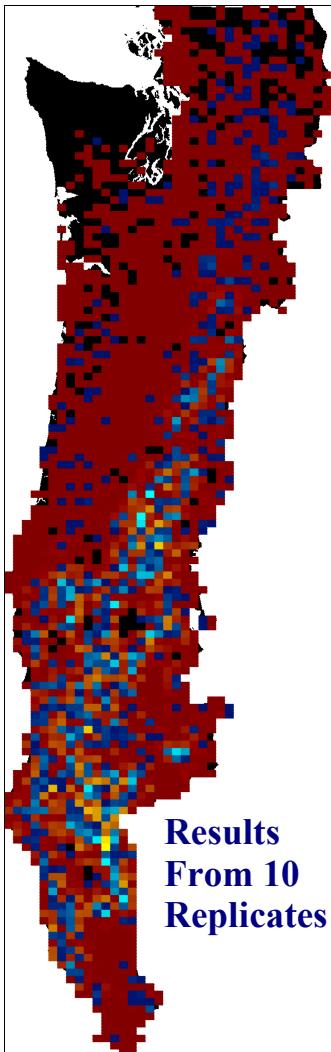
Habitat Quality



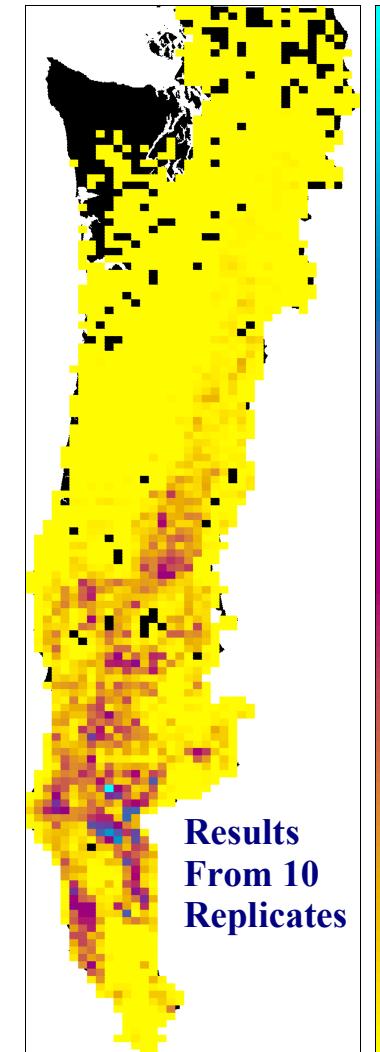
Dispersal Flux



Productivity



Stable Distribution



Results
From 10
Replicates

Best Source

Highest Flux

Lowest Flux

Worst Sink

Results
From 10
Replicates

Highest Occupancy

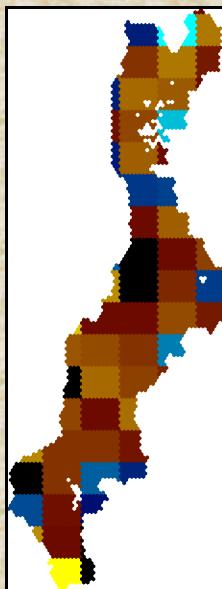
Lowest Occupancy

5 National Forests Functioned as Sinks

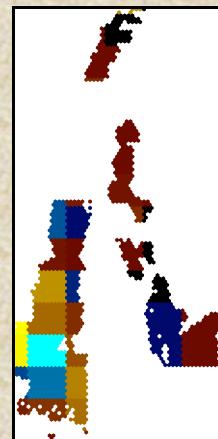
Most Severe Sink



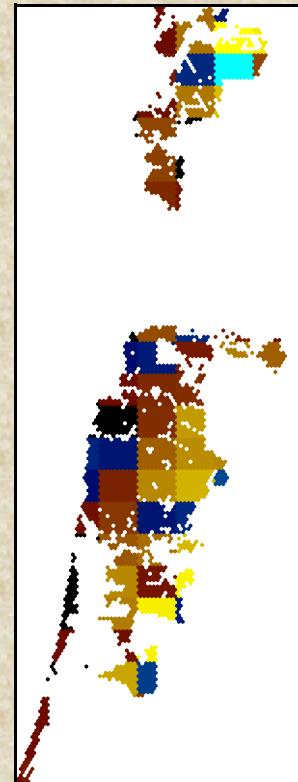
Deschutes



Winema



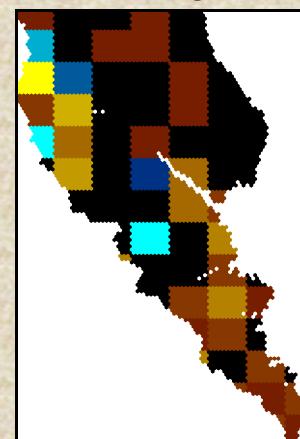
Siuslaw



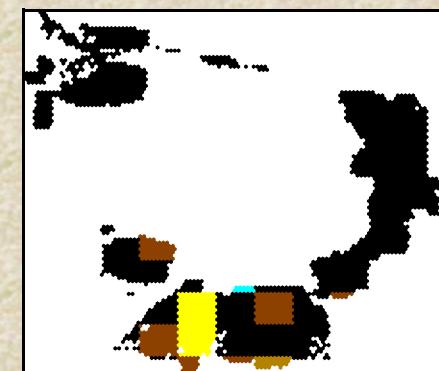
Most Benign Sink



Okanogan



Olympic



Productivity (10 replicates)

Worst Sink

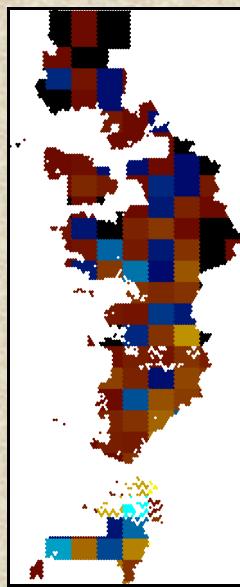
Neutral

Best Source

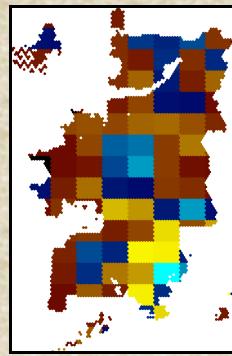
Weakest Source



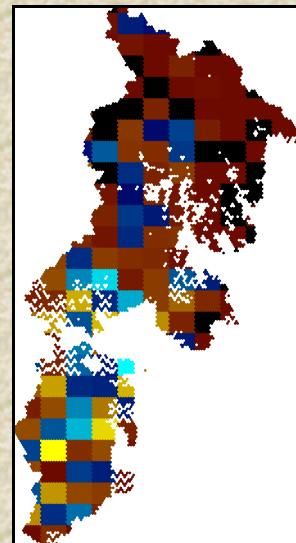
Mount Baker-Snoqualmie



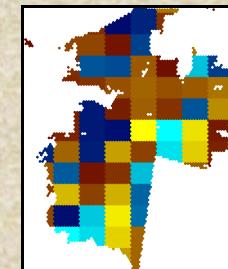
Gifford Pinchot



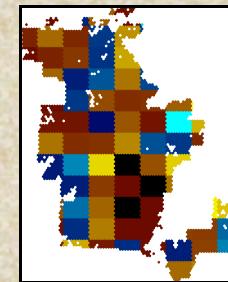
Wenatchee



Mount Hood



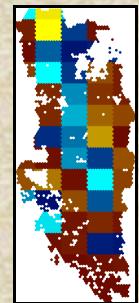
Siskiyou



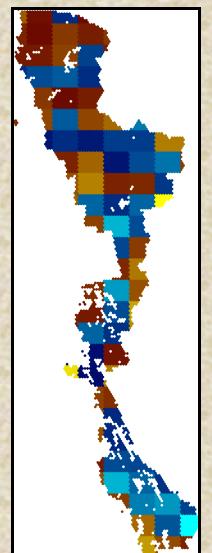
Willamette



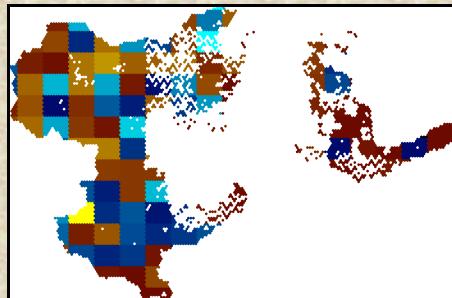
Mendocino



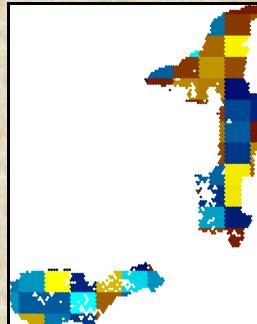
Six Rivers



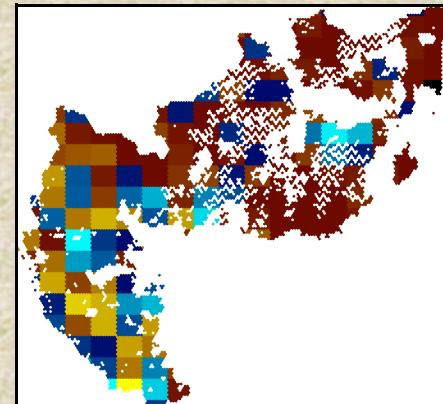
Klamath



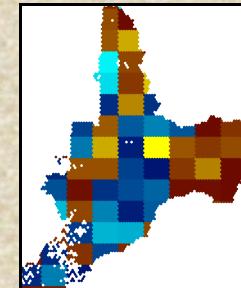
Rogue River



Shasta-Trinity



Umpqua



Productivity (10 Replicates)

Worst Sink

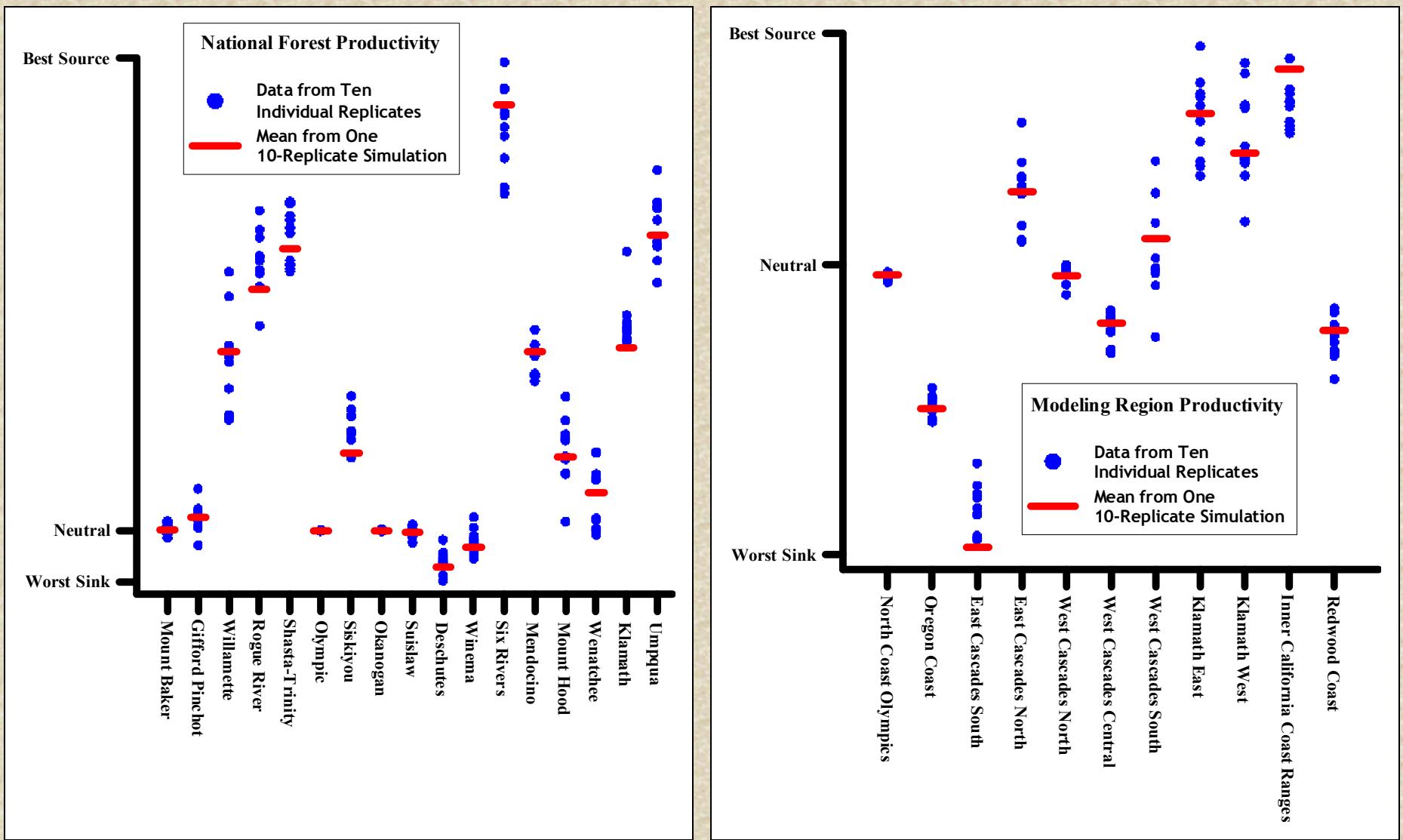
Neutral

Best Source



Strongest Source

Productivity and Variability by National Forest and Modeling Region



Projection Matrix Showing the Probability of Making Excursions between National Forests

| | Mount Baker | Gifford Pinchot | Willamette | Rogue River | Shasta-Trinity | Olympic | Siskiyou | Okanogan | Suislaw | Deschutes | Winema | Six Rivers | Mendocino | Mount Hood | Wenatchee | Klamath | Umpqua |
|-----------------|-------------|-----------------|------------|-------------|----------------|---------|----------|----------|---------|-----------|--------|------------|-----------|------------|-----------|---------|--------|
| Mount Baker | 0.9110 | 0.0001 | -- | -- | -- | -- | -- | 0.0083 | -- | -- | -- | -- | -- | -- | 0.0153 | -- | -- |
| Gifford Pinchot | 0.0004 | 0.9461 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 0.0016 | 0.0056 | -- | -- |
| Willamette | -- | -- | 0.9501 | 0.0000 | -- | -- | -- | -- | 0.0001 | 0.0381 | -- | -- | -- | 0.0190 | -- | -- | 0.0176 |
| Rogue River | -- | -- | 0.0000 | 0.8532 | -- | -- | 0.0087 | -- | -- | 0.0000 | 0.0560 | -- | -- | -- | -- | 0.0175 | 0.0199 |
| Shasta-Trinity | -- | -- | -- | 0.0000 | 0.9157 | -- | -- | -- | -- | -- | -- | 0.0325 | 0.0130 | -- | -- | 0.0115 | -- |
| Olympic | -- | -- | -- | -- | -- | 0.7083 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| Siskiyou | -- | -- | -- | 0.0066 | -- | -- | 0.9122 | -- | -- | -- | -- | 0.0026 | -- | -- | -- | 0.0046 | -- |
| Okanogan | 0.0001 | -- | -- | -- | -- | -- | -- | 0.8738 | -- | -- | -- | -- | -- | -- | 0.0002 | -- | -- |
| Suislaw | -- | -- | 0.0000 | -- | -- | -- | 0.0000 | -- | 0.8692 | -- | -- | -- | -- | 0.0000 | -- | -- | -- |
| Deschutes | -- | -- | 0.0052 | 0.0001 | -- | -- | -- | -- | -- | 0.8989 | -- | -- | -- | 0.0000 | -- | -- | 0.0005 |
| Winema | -- | -- | -- | 0.0158 | -- | -- | -- | -- | -- | 0.0000 | 0.8823 | -- | -- | -- | -- | 0.0000 | 0.0000 |
| Six Rivers | -- | -- | -- | 0.0000 | 0.0234 | -- | 0.0060 | -- | -- | -- | -- | 0.9000 | 0.0082 | -- | -- | 0.0276 | -- |
| Mendocino | -- | -- | -- | -- | 0.0062 | -- | -- | -- | -- | -- | -- | 0.0042 | 0.9420 | -- | -- | -- | -- |
| Mount Hood | -- | 0.0023 | 0.0059 | -- | -- | -- | -- | -- | -- | 0.0001 | -- | -- | -- | 0.9487 | -- | -- | -- |
| Wenatchee | 0.0399 | 0.0041 | -- | -- | -- | -- | -- | 0.0094 | -- | -- | -- | -- | -- | -- | 0.9441 | -- | -- |
| Klamath | -- | -- | -- | 0.0269 | 0.0063 | -- | 0.0090 | -- | -- | -- | 0.0001 | 0.0214 | -- | -- | -- | 0.9011 | -- |
| Umpqua | -- | -- | 0.0230 | 0.0309 | -- | -- | -- | -- | -- | 0.0074 | 0.0001 | -- | -- | -- | -- | -- | 0.9252 |

Conclusions

Preserving Detail and Realism

- Can use multiple sampling schemes and spatial scales
- Sampling schemes do not have an affect on simulation
- Retain as much complexity in simulations as you want

Understanding Complex Systems

- Quantifies source-sink behavior and connectivity
- Illustrates how source-sink dynamics and connectivity are really different ways of viewing the same process

Hopefully this methodology will prove to be a valuable complement to the suite of existing tools already in use...